

THE CRATAEGUS PROBLEM

ERNEST J. PALMER

IN LOOKING OVER the field of American taxonomic botany, as judged by the manuals, reports, and local plant lists that have been published since the beginning of the present century, it must be apparent to any one that the biggest unsolved problem and the one about which the greatest difference of opinion exists is that of the genus *Crataegus*, especially as regards the validity of the large number of species that were proposed, mostly during the first decade of the century.

There can be little wonder that when the twenty or twenty-five supposedly well-known species of the older manuals began to expand by scores and hundreds, until more than a thousand new species and varieties had been published, the first feeling of surprise on the part of the general students of botany and interested laymen, later assumed something like an attitude of dismay and incredulity, as they realized the hopelessness of attempting to become acquainted with or to identify living plants and collections of this genus from technical descriptions, in many of which only very slight characters were indicated to differentiate the proposed species.

In Gray's *Field, Forest and Garden Botany*, published in 1857, twelve species and two varieties of *Crataegus* were listed for the states east of the Mississippi River. This included native and cultivated Thorns. Ten species and four varieties, native and introduced, were recognized in Gray's *Manual of Botany*, that appeared in 1867. In 1860 Chapman published his *Flora of the Southern United States*, in which descriptions were given of eleven species and one variety, most of them being the species of Gray's *Manual*, with only three additions. Four species were mentioned in Coulter's *Manual of Rocky Mountain Botany*, in 1885. Three years later Focke, in Engler and Prantl, estimated that there were about 30 or 40 species of the genus growing in the North Temperate Zone. The Sixth edition of Gray's *Manual*, the last to appear in the 19th century, was published in 1889, and in this work only ten species and four varieties of *Crataegus* were recognized for the *Manual* range.

Up to the year 1899 about 175 names, including varieties and forms, a number of them merely on garden lists and without botanical descriptions, had been published for North American

Crataegi. A large proportion of these were segregates of supposedly polymorphic species, such as *C. crus-galli*, *C. coccinea*, *C. punctata*, *C. glandulosa*, *C. tomentosa*, and others.

About ten years later what may be called the period of expansion for the genus began. In 1899 and 1900 Beadle and Ashe published independently descriptions of several new species from the southeastern United States, followed quickly by many others, and Sargent a year or two later began describing many new forms, mostly found in the Northeastern and Central States. Altogether Mr. Ashe has published at least 177 species and 3 varieties of *Crataegus*, Mr. C. D. Beadle 143 species and 1 variety, and Professor Sargent more than 700 species, 22 varieties and 5 forms. A small number of Sargent's names were new combinations or were proposed as substitutes for various reasons for his own previously published species or for those of others.

The treatments of the genus that have appeared in the manuals and local floras since this period of expansion began have all been admittedly provisional and partial, with frequent shifting of ground in regard to the species recognized and the passing over entirely of many others. This is not surprising nor a matter for adverse criticism, but it serves to illustrate the difficulty of the problem.

Most compilers of local lists have in the meantime given up entirely any attempt to enumerate the Thorns of their regions, and have simply mentioned the fact that various unrecognizable species occur; some have referred their readers to the manuals or other general treatments, or have submitted collections to a few institutions or students of the genus who were willing, or who had the temerity, to undertake identifying them. The Arnold Arboretum has been called upon to pass upon a number of such collections, and in spite of the large number of types and the great amount of other material in the herbarium, as well as an extensive collection of living plants and ample literature available here, it has in many cases been a difficult matter to make determinations of some of the specimens, even when flowers or fruit were present, and in most cases it is quite out of the question to determine them from sterile specimens or from a single leaf or flower, as can often be done in such groups as the Willows, Oaks, Maples, Roses, and many others.

As a result of this situation a feeling seems to have arisen among many unprofessional and uncritical students of plant life, and even amongst some botanists, especially those not mainly concerned with taxonomy, that a hopeless confusion exists in this genus and that most if not all of the recently proposed species are

without standing and should be disregarded. It has also been suggested that the genus is in a state of mutation or instability or that the different forms have been so frequently hybridized with each other that no clear specific lines can be drawn as in other genera, and that almost any individual tree might be made the type of another so-called species.

Such a situation as the present is obviously unsatisfactory and unscientific, but much of the uncertainty and skepticism, understandable as it is, does not seem to be entirely warranted by the facts. For it is probably true that morphological characters peculiar to and inheritable in segregable groups of individuals that we call species are generally as constant and well marked in this genus as in many other genera of the *Rosaceae* or other families, such as *Rubus*, *Rosa*, *Prunus*, *Cotoneaster*, or *Rhododendron*. The main difference and difficulty in regard to *Crataegus* as contrasted with such other genera is that of size, the very large number of species that must be dealt with in any adequate general treatment, their wide geographical range, and the practical difficulties of studying or collecting them in the field, with the uncertainties of seasons and irregularity of fruit crop, or of bringing together under cultivation a collection at all adequate for a general revision. But in addition to this it will be generally agreed, I believe, that matters have been greatly complicated by the way in which the genus has been treated in the past in botanical literature, many of the older names having been published without recognizable descriptions or definite data as to where the plants to which they applied originated. And in regard to the much larger number of species that were distinguished later, although these were generally accompanied by fuller descriptions, much uncertainty exists because they were in many cases based upon very slight differences separating them from others, and perhaps sometimes without sufficient field study to determine the constancy of their distinctive characters, or without sufficiently careful comparison with previously described species to which the material might have been referred with a broader conception of species, under which plants with slight but evident distinctive characters might have been treated as varieties or forms of the more outstanding species.

It has long seemed to the writer that, for practical reasons, such a conservative treatment, in dealing with as large a genus as *Crataegus*, is most desirable, and studies with this in view both in the field and at the Arnold Arboretum have been in progress for several years.

In view of the great amount of work done upon the genus by

the late Professor Sargent and the accumulation of material and literature in the herbarium, plantations, and library here, it seemed evident that the Arnold Arboretum was the logical place for initiating and carrying out such a work, and indeed, that it could scarcely be done with adequate facilities anywhere else. And for this reason, after being urged to do so from a number of sources, the writer rather reluctantly undertook this difficult and somewhat formidable task.

The collection of *Crataegus* in the herbarium here is without doubt the largest and most complete in existence, and although it, naturally, does not contain specimens of all the forms of Thorns that have been described, the approximately 25,000 sheets from all parts of North America, including all of the type material of the species described by Sargent as well as isotypes of many others, have been assembled to represent as fully as possible the geographic range as well as the morphological characters and the behavior under cultivation of as many species as were obtainable.

At the beginning of Professor Sargent's intensive study of *Crataegus* he initiated the plan of planting seeds from the type tree, and from other specimens, of each of his newly described species, as well as of those previously known, and of many others from which herbarium material had been collected but which had not yet been determined. This plan has been continued, and in the thirty years that have elapsed since its beginning the plantation has grown into a collection at the present time of about 1,400 labelled trees of record, representing nearly 700 species and varieties, only a small percentage of which are of Old World origin. Other species that were grown, many of them to maturity, are no longer living, but herbarium specimens of them have in most cases been preserved. The plantation on Peters Hill at the Arboretum is now probably the largest living collection of any single genus of woody plants, or at least of trees, that has ever been brought together for the purpose of scientific study.

A critical study of the trees of this collection and a comparison of them with the herbarium specimens and record of the native parent plants from which the seed was taken has been in progress for several seasons, and it is expected to throw valuable light upon the status and relationship of many species. With this evidence it will be possible for the first time to determine in many cases whether the distinctions upon which the described species were based are constant or are merely individual variations, as well as to arrive at more definite conclusions as to the relative value of such characters as pubescence, the number of stamens and styles,

color of the anthers, shape and color of the mature fruit, &c., as specific criteria.

To examine and make notes upon this large number of trees both in the flowering and fruiting stage and to make the necessary comparisons with the herbarium material and with the published descriptions, is at best a slow process and one attended with some practical difficulties. Most of the trees have now grown to fruiting size but not all of them produce flowers or fruit each year, some seasons being quite unfavorable to the less hardy forms. Others are just coming to maturity and some flower for the first time each year. Since the flowers are very transient and it is possible to determine the color of the anthers for only a short period after they open, the season often advances so rapidly that it is difficult to keep up with them in this stage. Additional field work which is urgently needed in this genus in many parts of the range also presses at this season and for several years it has made it impossible for me to be at the Arboretum in spring.

It should also be understood that large as the collection here is, and furnishing as it does by far the best experimental data so far available, it is by no means complete or fully adequate for a study of the whole genus. Some species of the southern states have not proved hardy in this climate and for various reasons many which have been started have not survived and others have not been secured. It can easily be understood that a certain amount of error was almost unavoidable in the various steps from collecting herbarium specimens and seeds in the field, planting and germinating these, transplanting the seedlings to nursery rows, and finally to a permanent place in the collection, as well as later in keeping records and in having the plants properly labeled. A small percentage of such errors have been detected in the collection here. Some of these are so obvious as to be unmistakable and sometimes correctable, but in a few cases they may leave open to doubt questions of possible variability, which we would like to settle. In addition to this the first idea of the plantation, which seems to have been merely to illustrate the different species by typical specimens, was scarcely broad enough to furnish conclusive evidence such as might be desired to decide in some doubtful cases. It was of course impractical to attempt to grow a large number of each of the several hundred supposed species to fruiting size, but it would have been most helpful if this had been done in a few selected cases at least.

The main region of distribution for *Crataegus* in North America extends from the Atlantic seaboard to beyond the Mississippi

river, and the border of the plains. The western boundary may be roughly taken as running from northwestern Minnesota, through eastern Nebraska, Kansas, and Oklahoma, to the mouth of the Colorado river in Texas. Many of the species and several of the groups disappear much farther east, and several sub-regions may be recognized. West of this region *Crataegus* is a genus of minor importance and such scattered species as occur are mostly quite different and distinct from those of the east, and the problem is comparatively simple. Some of the western species are associated with the Sonoran floras and range southward into Mexico, and others belong to the Rocky Mountains and Pacific floras.

A considerable part of this main area has been pretty thoroughly explored, but it should be remembered that there are still large sections of the country in which very little collecting has been done and where the *Crataegus* flora is still inadequately known.

Most of the material studied by Sargent and other recent authors was brought together as a result of intensive collecting by local students in a comparatively few limited areas. A large amount of material was left undetermined in the herbarium here, and while much of this has recently been placed with described species, a number of collections remain, with either complete or partial material, that cannot be so disposed of, and reluctant as one might be to add to the number already published, it will be necessary to describe some of these that seem clearly distinct.

The sections of North America where the *Crataegus* flora is best known and from which material is fairly adequate are the St. Lawrence valley, most of New England, New York, Pennsylvania, and parts of the Southeastern and Middle-western States and the Rocky Mountain and Pacific States. Additional field work is particularly needed in parts of Ohio, Michigan, Wisconsin, Minnesota, Iowa, Arkansas, Tennessee, Oklahoma and eastern Texas, as well as in the Piedmont regions of the Gulf States. But while there is every reason to believe that some new species and varieties will turn up in these regions, it is not likely that the number that cannot be referred to forms already known will be large.

There are doubtless many questions in regard to the genetic relationships and the ideal classification of *Crataegus*, as in other plant groups, that cannot be definitely settled on purely morphological grounds. Experimental growing of seedlings on a large scale, cross-breeding, and cytological study of the chromosomes, as well as of the physiology, histology and pathological responses of the supposed species will ultimately throw much light upon some of these, and may greatly modify our present systems of classi-

fication and conception of species. Investigations along some of these lines are now in progress at the Arnold Arboretum and elsewhere, but the practical difficulty of applying such tests to hundreds of forms of such slow-growing plants as *Crataegus* is obvious. According to Mr. W. H. Judd, propagator for the Arboretum, the seeds require from two to six years to germinate. And on an average ten years more must elapse before they grow to fruiting size.

But valuable as such investigations are, they have not yet progressed far enough, at least in the case of *Crataegus*, to be used as the basis for any scheme of classification. And indeed it scarcely seems likely that they can ever be so used except in a limited way, or that any classification based mainly upon other than obvious morphological characters can be devised that will be practicable and usable by the large and increasing number of people of all degrees of scientific attainment who are for various reasons interested in the study of plants. Of course a taxonomic arrangement based upon morphological characters should, approximately follow lines of genetic relationship, but in certain cases it probably does not do so consistently, and as in keys used in the manuals to aid in locating species, an artificial arrangement is sometimes more useful and usable than one that is concerned only with natural relationship.

In considering any scheme of classification it is well to understand clearly what the writer means by the term species or other subdivisions of the group, for there is still nothing like uniformity in the use of such terms. If we begin by recognizing that there is nothing inviolable or sacrosanct about a species, but that it is merely a convenient unit to be employed in describing a group of plants or animals having a number of recognizable characters in common, and that the limits of such a unit must be based upon the best judgment of some competent observer who has studied the group, it is evident that a considerable degree of latitude may be exercised in the use of the term. The number of species in any group will therefore vary according to whether the author takes a narrow or a broad view of the species. The decision must be more or less arbitrary, and naturally there will be room for differences of opinion about any proposed classification, and in the nature of things it must be somewhat provisional and subject to revision. It might be more accurate to refer to such units as morphological species, since they may differ greatly in limits and numbers from the species concept of the geneticist or cytologist.

A system of classification in which only species are recognized, and

one in which consequently only Linnaean binomials need be employed, has its obvious advantages in simplicity, especially in small groups. But to attempt to treat such a large genus as *Crataegus* in this manner would result either in an enormous and unwieldy number of species, or specific lines would have to be drawn so broadly and with so many exceptions as to make them almost useless. A conservative treatment, such as seems desirable here, should regard as species all readily recognizable forms that can be distinguished by a group of characters or at least by more than one clear difference, with descriptions broad enough to allow for a reasonable amount of individual variation, to be determined by observation. Under varieties would be placed such subdivisions of the species as differ from the typical form of the description in a single clearly recognizable character or in one or more minor details. And in some cases it might be desirable to give names to forms in which a single distinguishing character less clear or constant is found.

Under such a treatment the number of species might be considerably reduced from the present total, but it would still be large, probably much larger than in any other genus of woody plants in the American flora, unless we refuse arbitrarily to recognize as species forms quite as well marked as many of those generally so treated in other genera. Such a course would go far towards defeating its own purpose.

Although no satisfactory general treatment of *Crataegus* has yet appeared since the publication of the large number of recently proposed species, some progress has been made towards a better understanding of the genus. New combinations have been made by Mr. Eggleston and others reducing a large number of species to varietal rank, and many others have been treated as synonyms. In many cases the view taken is probably correct and constitutes a real contribution, but in regard to others there seems to be very good ground for maintaining them as species, based upon our observations here. This is quite understandable, since it is not likely that any two students working critically on so large a group could agree in all cases. It must also be admitted that some provisional treatment short of recognizing all of the hundreds of newly described species was urgently needed for the general manuals, and that on the whole the space given in them to this genus was as large as could have been expected. Still it is not possible to limit the number of species in a genus by law or rule, desirable as this might be in some respects. And we, therefore, have felt here that it will be better to proceed slowly and to collect as much data as possible before attempting a revision.

Sufficient progress has been made in observing the living collections at the Arboretum, in additional field work and in rearranging and critically studying the material in the herbarium, to make it possible to draw a few general conclusions.

The extreme complexity of the genus, the existence of many distinct forms in all parts of North America, many of them being quite local in range, and which were unrecognized and unaccounted for in the older manuals and floras, has been amply demonstrated. The recognition of this fact and the great amount of work done in making them available for study both through published descriptions and cultivation constitutes a great contribution on the part of Sargent and his co-workers and contemporaries. It cannot be too strongly emphasized that nearly all of the large number of forms described were based upon real differences. Whether these differences were sufficient to be made the basis for specific distinctions is an open question about which there can properly be much difference of opinion. In the opinion of the writer it might have been better in many cases to have treated them as varieties or forms or merely as variations of polymorphic species.

The specimens cultivated at the Arnold Arboretum show generally that the distinctive characters of the wild specimens, which were taken as the basis for the new species hold true often to the minutest particular. There are a few exceptions to this.

Besides the plantations at the Arnold Arboretum a very large number of species were grown and records kept of them by the Park Department of Rochester, New York. The collection there is available for study, and those who have been in charge of it report similar results, and indeed some of them are much more inclined to recognize and to insist upon the distinctiveness of the species than we are.

In addition to those species that can probably be more properly treated as forms or varieties, some others were published of which the names were invalid, or which cannot be maintained for various reasons. In some cases names were preoccupied or the same name was used more than once for different species by the same or by different authors. Most of these cases have already been corrected but apparently a few still remain. Duplicate descriptions undoubtedly sometimes appeared of the same plants, either by the same or by different authors working independently. This was almost unavoidable from the mass of material that was being handled, the rapidity with which the descriptions appeared, and the small amount of tabulation that had been done, as well as because the characters of some of the sections into which it has been proposed to divide the genus were not properly understood.

There is a very wide range in the variability of the leaves, flowers, fruit and several others characters in *Crataegus*, and the species can be arranged in several natural sections or groups. There have been a number of attempts at dividing the genus into these sections, with considerable variation as to the number, arrangement and limits of the groups. The oldest arrangement is that of Loudon in 1838.¹ In this treatment, he arranged the species of which he gave description in 15 sections, of which one (XV. *Pyracantha*) is not now included in the genus. Four others, his sections V. *Nigrae*, X. *Azaroli*, XI. *Heterophyllae*, and XII. *Oxyacanthae*, are exclusively Old World groups. His other sections are clearly recognizable and most of the names are retained, with a few changes in the placing of species. The sections of American Thorns were I. *Coccineae*, II. *Punctatae*, III. *Macracanthae*, IV. *Crus-galli*, VI. *Douglasii*, VII. *Flavae*, VIII. *Apiifoliae*, IX. *Microcarpae*, XIII. *Parvifoliae*, and XIV. *Mexicanae*. To these a number of new sections have been added by later authors.

Mr. Eggleston in his treatment of the genus in the 7th edition of Gray's Manual (1907) arranged the American species that came within the geographical range of that work into 17 sections, and in the 2nd edition of Britton & Brown, Illustrated Flora (1913) he has 15 sections, some of them slightly changed in scope from the former treatment.

Professor Sargent proposed several new sections, and in his last treatment, in the 2nd edition of the Manual of the Trees of North America (1922) he arranged the arborescent species into 20 natural groups, which did not take into account the Mexican species nor the two exclusively shrubby groups, *Parvifoliae* (*Uniflorae*) and *Triflorae*. In the course of his studies of the genus he abandoned his groups *Lobulatae* and *Flabellatae* and seems to have changed his view regarding the groups *Coccineae* and *Rotundifoliae*, as well as to have accepted Beadle's name *Silvicolae* as having priority over his *Medioximae*, and *Macracanthae* of Loudon for *Tomentosae*.

Mr. Beadle, in his generally excellent treatment of the species of the southeastern United States, as it appears in the 2nd edition of Small's Flora, has carried the division of the genus into sections to an extreme degree, basing some of them, as it seems to me, upon characters of no more than specific value, and in the case of the *Crus-galli* and *Berberifoliae* scarcely that in some cases. Thirty-three sections are recognized in this work, which covers less than a third of the area of the United States.

The sections differ considerably from each other in their dis-

¹ LOUDON, J. C. Arboretum et fruticetum britannicum, II. 813-867 (1838).

inctiveness and in the constancy of the characters by which they can be recognized. It is generally possible to definitely place most species in the proper group with the help of keys or by one familiar with them, but in most cases there is an indistinct border line where one group merges into another, and perhaps into more than one in different directions or in different areas, and it is difficult to say whether certain species belong with one or with the other. This may indicate either hybrids between species of the different groups, which is sometimes probably the true explanation, or it may indicate merely the relationship of the groups to each other and that certain intermediate species connect them. For example, in the section *Crus-galli*, which is generally one of the best marked of the larger groups, some species approach in the character of their fruit and foliage those of the section *Punctatae*, which is usually placed next to it, and in other species, the thinner or slightly lobed leaves and smaller fruit, which may finally become mellow or succulent, or in the thinner, scaly, bark of the trees, an approach to the *Virides* is found. The *Virides* group has good distinguishing characters in most cases, but besides certain species that seem in some ways intermediate with the two previously mentioned, some of the species assigned to the *Pulcherrimae* in the southeastern states have certain resemblances to this section, and in southeastern Texas species have been found that seem intermediate between *Molles* and *Virides*. There has been much uncertainty about the *Coccineae* group. Loudon obviously intended to take *Crataegus coccinea* L. as the type of this. The illustration he gives for the typical form of that species suggests some large-leaved form of such a species as Sargent's *Crataegus pedicellata*, but the description he gives seems to have been drawn from several forms that have later been considered as distinct, probably including *C. mollis*. It also is difficult and perhaps impossible to tell what Linnaeus' species was, as that too appears to have included two or more distinct things. It is not an unnatural consequence that later authors have been much confused and very hazy in the interpretation of this species, and indeed it has since been made to include either typically or as varieties, forms of many diverse species of American thorns. The group *Coccineae*, as finally used by Sargent, includes several species of the northeastern United States and Canada, having rather large, thin leaves, mostly glabrous when mature, flowers in which the styles are usually less than five, and fruit with rather small, sessile calyx, and flesh that becomes pulpy or succulent at maturity. On the one side this group approaches the *Tenuifoliae* and on the other the *Molles*, and although,

as in other cases, it is difficult to decide definitely to which of these groups certain species belong, a description broad enough to cover such a wide diversity of forms as have been included under this group and the *Molles*, as well as those of the small *Dilatatae* group of Sargent, would lose much of its taxonomic value.

The same situation seems to obtain with most of the other groups, which it is not necessary to take up in detail here. Attention may be called, however, to the fact that there are several small groups, such as *Aestivales*, *Brachyacanthae* (*Brevispinae*), *Microcarpae* and *Cordatae*, which appear to be so clearly distinct that they probably represent species that originated quite early in the history of the genus.

It seems probable that *Crataegus* was a comparatively early offshoot from the *Pomaceae* stock, but that its principal development has taken place since the Glacial periods of the Quaternary and even in very recent times. It may have originated at rather high latitudes in Eurasia in a period of favorable climatic conditions and been dispersed from a circumpolar center southward into both hemispheres before the close of the Tertiary era. This view seems to be supported by its present wide distribution and that of associated plants, and by the fact that the genera most closely related to it amongst living plants, such as *Osteomeles*, *Cotoneaster*, *Pyracantha* and *Mespilus*, are confined to the Old World. That the groups found in the two hemispheres are all, or nearly all, quite distinct would also indicate a considerable period of isolation.

Paleontological evidence seems to be rather meager for a genus so abundant and widely distributed at present, but a number of fossil species have been described, based upon either leaves or fruit, from both the Old and New World. A comparison of these with living species will be of value and may throw light upon the present distribution and relationship of the different groups.

A few generalizations can be made as to the geographic distribution of the groups and some of the species in America, and its significance.

A large proportion of the species that have been described appear to be quite local and in not a few cases the only material known is that from the type locality or from a single tree. Such species, when they come from regions that have been pretty well explored botanically, naturally fall under suspicion as to their validity, and many of them will probably prove to be only divergent forms or hybrids. Many species, however, and some of them well marked ones, are of quite restricted range. This may be accounted for in two ways: either they are comparatively recent forms that have

not been able to spread far from the point of origin, or they may be relics of ancient and disappearing types. In the case of *Crataegus* the former seems much the more probable explanation. Several considerations lead to this conclusion, but it need only be mentioned here that in the case of relic species the range is usually interrupted and they crop out in peculiarly protected or favorable spots, often widely separated from each other. This is not the case in *Crataegus*, with a very few exceptions, so far as known.

Most species of *Crataegus* are more or less pronounced calciphiles, and they are found in the greatest diversity and abundance in limestone regions. Many of them are limited to such outcrops, and the soil factor is probably an important one in determining their distribution. There are, however, some striking exceptions to this. There is a marked zoning of the groups from north to south, and to the westward they are limited by aridity, like other mesophytic plants, as they approach the plains. But there are various other minor causes, besides soil and climate that serve to limit them and that have brought about the present distribution. This is emphasized by the fact that in spite of the limits of the groups north and south in nature, the species in the main seem quite adaptable in the matter of climate, many of those native to Florida and southern Texas having proven hardy in New England.

The genus as a whole is not adapted to spreading in forest areas, and most species are essentially plants of prairie openings, borders of woods, copses, pastures and glades, or along the open banks and bluffs of streams. In primitive times such habitats in Eastern North America, where other conditions were favorable, were not of wide extent. The great unbroken forest that extended from the Atlantic coast, across the Mississippi valley, to the edge of the plains, afforded only occasional opportunities for the growth of such small trees and shrubs, and in places where they might seek to gain a foot-hold they were probably held in check by frequent fires and by grazing animals, since the young shoots, before the spines are sufficiently developed to afford protection, are eagerly eaten by the ruminants. The seeds are heavy and are not likely to be transported far except when carried by water or in the stomachs of birds and other animals. The latter seems to be an important means for their dissemination at present, but so long as favorable localities were lacking this would avail little, and their advance was also probably impeded by the slow germination of the seeds.

Since the clearing away of the forest on such a large scale, vastly greater areas have become available and there has undoubtedly

been a great increase in their development and in the spread of species in recent years.

The distinct calciphiles and rock growing species, or those of more specialized requirements, are usually the most limited in their range, and the more widely distributed ones, such as *Crataegus crus-galli*, *C. punctata*, *C. viridis*, *C. apiifolia*, *C. spathulata*, *C. Margaretta*, and *C. tomentosa*, are such as grow in alluvial ground or that follow the courses of large drainage basins.

In general it may be thought that the more widely distributed species are the ancient ones, or that at least they are not of very recent origin. The criterion of age and origin is probably, however, only partly reliable in this genus, since other factors, as pointed out, have served to aid or retard their extension. In the writer's opinion the groups *Aestivales*, *Brachyacanthae* and *Mexicanae* are probably most closely related amongst American Thorns to the primitive types, and none of these have a particularly wide geographical range. In the case of *Aestivales*, at least, this may be due to the peculiar and limited habitat. And it is probable that all of them are retreating or disappearing groups.

A striking exception to the usual soil preference and habitat of most of the groups is afforded by the large association of forms which has been classed under *Flavae*, although Mr. Beadle divides them into twelve or fourteen sections, of which it may be desirable to maintain some. These are restricted to the southeastern United States, where they are very abundant, and they are for the most part decidedly oxylophiles, inhabiting dry, sandy, upland woods, or areas occupied also by a peculiar stunted shrubby flora, known as "scrub" in Florida, where the soil is a deep fine deposit of nearly pure sand. Typical trees of this group have quite a distinctive habit of growth. The older trunks are clothed with a thick dark bark which is deeply fissured and cross-checked into small blocks, much as in *Cornus florida*, *Diospyros virginiana* or *Viburnum rufidulum*. The stiff, curved, branches are usually terminated by slender branchlets, which are either zig-zag or pendulous, and thickly set with single or small clusters of flowers and the foliage and inflorescence is extremely glandular. Other exclusively southern groups are the *Pulcherrimae*, *Triflorae* (*Bracteatae*), *Microcarpae*, *Brachyacanthae*, and *Aestivales*.

Uncertainty concerning the characters and limits of some of the groups, and the actual difficulty of determining to which group certain species belong seems to have been the cause of some confusion in the past and may have been responsible in some cases for the duplication of descriptions of identical plants, which can

be properly placed when brought into comparison with each other.

How far the matter of hybridization enters into the problem of the complexity and proper classification of *Crataegus* is a puzzling one, and one that cannot be settled definitely without a great deal more experimental work being carried on systematically through many years.

From what is known of the rather frequent cases of hybridization amongst other Rosaceous genera, and from the fact that several supposed hybrid species of *Crataegus*, as well as a cross with the closely related genus *Mespilus*, are in cultivation, and others are found growing spontaneously that suggest such an origin, it is almost impossible not to believe that natural hybrids do sometimes occur. Anyone who has been in a large growth of *Crataegus* in early summer, where many diverse forms are growing together, and several of them blooming simultaneously, with the wind carrying pollen, and with swarms of busy insects flitting from one flower and tree to another, can easily see how this might come about.

At the same time it must be remembered that there are many ways in which the integrity of species is protected in nature, and if this were not so, the numerous distinct forms that are found in many large genera could never have been segregated or maintained. Slight physiological differences are often enough to insure immunity, and in the case of *Crataegus*, where the period during which fertilization can be effected is very short, a difference of only a day or two in the ripening of the pollen and the receptivity of the stigmas may make cross-pollenization in the wild state unlikely or impossible.

But in addition to the theoretical considerations that lend support to the belief in *Crataegus* hybrids some positive morphological evidence is found both in the intermediate characters of certain forms growing with others that may be the parent species, as well as in the high percentage of pollen sterility.

Standish,¹ who examined the pollen of 171 species, states that thirty-five of this number had normal pollen, sixty, from 10 to 50% sterility, forty-one, from 50 to 75%, and thirty-five from 75 to 100%. This would seem to indicate a large percent of hybrids or chromosome irregularity.

Longley,² who made studies of the chromosome structure, classes as diploids thirteen of the eighty-one species recorded, fifty-seven as triploids, and eleven as tetraploids and triploids. A considerable

¹ STANDISH, L. M. What is happening to the Hawthorns? (Jour. Heredity VII. 266-279. 1916.)

² LONGLEY, A. E. Cytological studies in the genus *Crataegus*. (Am. Jour. Bot. XI. 249-282. 1924.)

degree of variability in the seedling offspring of triploid or tetraploid species might normally be expected. But this, as stated above, has not been the experience with the species grown here and elsewhere, where records have been kept. The fact that so large a percentage of the forms come true to the parent type scarcely seems to lend support to the theory that they are of hybrid origin, and if that is admitted to be the case upon other evidence, it would seem to indicate that these triploid forms have developed a type of apogamous reproduction, as pointed out by Sax,¹ and as a consequence do not develop the variations of usual hybrids. My colleague, Dr. Karl Sax, has kindly furnished me with the results of some preliminary experiments which he has conducted to test this. The anthers and stigmas were decapitated before opening in 25 to 50 flowers of a number of selected species. Of the 39 species and varieties reported on, 16, or 41%, set fruit, ranging from one or two in most cases, to five in *Crataegus erecta*, seven in *C. pruinosa*, and eleven in *C. Oxyacantha plena*. In an experiment of this character it is also possible that injury to the flowers may have reduced the chance of setting fruit in some cases. This would seem to indicate clearly that apogamous reproduction does sometimes occur, but as in the cases of the other lines of investigation upon chromosome characters and sterility, these experiments have not so far been carried out on a sufficiently extensive scale to be conclusive in regard to many species, although they point to general conclusions. As an illustration *Crataegus pruinosa* appears to be a well marked species with a wide range. Standish reports 60% pollen sterility in the specimens of this species tested. Longley found it to be a triploid, while Moffett² reports it as a diploid. It is possible that the specimens selected were not in some cases pure-bred *C. pruinosa*. And it can easily be seen that any modification in the scheme of classification, such as changing the limits of the section, transferring species from one to another, or combining several so-called species into one, might materially alter results and conclusions based upon them. To further illustrate this: Standish found a high percentage of sterility amongst species of the *Intricatae* group, and she concludes that it is closely allied to *Coccineae*, and that all of the species of *Intricatae* may have arisen as hybrids between two species of the latter group or between one such species and some other parent. However, the ranges of the two groups are quite different from those shown on the map used

¹ SAX, KARL. The origin and relationship of the Pomoideae. (Jour. Arnold Arb., XII. 3-22. 1931.)

² MOFFETT, A. A. A preliminary account of Chromosome behavior in Pomoideae. (Jour. Pomology, IX. 100-110. 1931.)

to support this conclusion. The two groups do overlap in the northeastern states, but the wide range southward and westward shown for *Coccineae* results from following the treatment in Gray's Manual, which includes *Molles* with that group, and if this were done consistently the range would be more than twice as extensive. Attention may be called to the fact in this connection that Longley found the three species of *Molles* examined to be diploids and all of the twelve *Coccineae* to be triploids. The range of the *Intricatae* group also extends westward through Ohio, Indiana, Kentucky, Michigan, southern Illinois, the Ozark region of Missouri and Arkansas to eastern Oklahoma, and many of the species are found outside the range of any species of *Coccineae* or in a few cases of any *Molles* species. Moreover, on morphological grounds, I can see little evidence of a close relationship between the *Intricatae* group and the *Coccineae*, as understood here. Whatever the origin of certain of the *Intricatae* species may have been, the group as a whole is one of the better, although not one of the best, marked natural sections, and it appears to be more closely related to the *Pruinosae* and *Rotundifoliae* than to *Coccineae*. There is at least ground for suspecting that conclusions as to the status of some of the other species might be modified if experiments were carried out on a larger scale or with more certainty as to the correct identity of the material used, although this might not change the general trend of the evidence.

Two points, however, seem clear: the need of a sound taxonomic basis for all lines of botanical work, and that any classification to be of practical value must be based mainly upon morphological characters.

Sax concludes, in his paper on the origin of the Pomoideae, that:

"On a genetic and cytological basis of classification all of the present genera of the Pomoideae might be classed as genetic species under one genus. In at least one case two genera should be combined under one species."

I think it safe to say that even our most conservative taxonomists and ardent "combiners" would scarcely approve of treating all of the forms of *Crataegus* of both hemispheres, including the genus *Mespilus*, as one polymorphic species.

Hybridization, therefore, seems to be a factor that must be reckoned with, but until much more experimental work has been done it is impossible to say how large a proportion of the recorded species, and in most cases which particular ones, originated in this way.

Where hybrids have arisen between two quite distinct and well

marked species or between those of two different groups, it may sometimes be detected by their intermediate characters or peculiar behavior, but this could only be done safely by careful field study and with data as to the species growing in the vicinity where the supposed hybrid originated, and as to the possibility of cross-fertilization. A hybrid between two closely allied species of the same group would be so obscure that they could scarcely be detected or identified on morphological characters, and to try to account for forms in this way, without experimental evidence, can be little more than a guess.

On the evidence available, as well as on theoretical grounds, it would seem then that the astonishing number of forms of *Crataegus* that have been detected and described are of diverse, and many of them probably of recent origin. First, there is a very large number of species and varieties that have arisen by what may be called, for want of more precise knowledge, the normal processes of evolution, and these can naturally be accounted for by the instability of triploid and polyploid species: second, there is probably a small number of hybrids between diploid, or between diploid and polyploid species, which may be expected to follow the Mendelian law of variability: and third, there is a perhaps larger group of hybrids between mostly triploid or polyploid forms, having pollen wholly or partly sterile, but which produce seed apogamously and therefore reproduce very closely all of the characters of the parent plants, thus fulfilling all of the evident requirements of normal species.

What disposition then should be made of the forms that have been described as species, of various degrees of distinctness and stability, a considerable number of which are probably of hybrid origin?

Since it has been found that the great majority of the forms grown from seed come surprisingly true to type, it seems to the writer that the practical thing to do in a general classification is to judge each recognizable form merely upon its morphological characters and where these seem sufficiently distinct to retain the specific name and treat it in all respects as a species, giving varietal rank to those less distinct. Where the evidence is available or as it becomes so, it will be desirable to indicate those species that are of hybrid origin, but the general student who is interested mainly in a workable basis for classification need not be greatly concerned with these.

The question of the relative value of the different morphological characters in diagnosing and describing species and varieties of *Crataegus* is also a debatable and perplexing one.

Professor Sargent placed strong emphasis upon the number of the stamens and the color of the anthers in distinguishing species, and Beadle, Ashe, and others also gave this as one of the key characters in many of their descriptions. So strongly was Sargent impressed with this, that in the writer's opinion, it was given undue value, and in some cases no other constant difference can be found between two described species except that of the number of stamens or the color of the anthers. Like many other characters, this seems to vary in constancy and value in the different groups and in different species within the groups. In the great majority of cases the seedlings which have been grown and studied here indicate that these characters come true with few exceptions, but that there are sometimes races or forms differing from each other only in the number of the stamens or the color of the anthers. This does not appear to me to be a satisfactory or sufficient distinction alone upon which to base species, although such races might be regarded as forms. The color of the anthers can only be determined in fresh material and for a few hours after the flowers open, and this is a practical disadvantage in using it as a key character in distinguishing species. But in some cases it seems to be the surest way of determining the identity of species where fresh flowers can be examined and mature foliage and fruit are not available.

In some species, and especially in some groups, pubescence on the foliage, young branchlets, inflorescence, or fruit is a valuable distinguishing character. But there are undoubtedly cases where this is variable and where there is both a glabrous and a pubescent form of a species. In some of the groups glands on the bracts, sepals, and leaves are abundant and conspicuous, while in some of the others they are rare or absent. This is often a valuable distinguishing character, but it is not always constant even within a species.

The size of the flowers, the number and arrangement in the corymbs, form of the ovary and calyx-lobes, the length of the pedicels and petioles, as well as the shape and serration of the leaves, are all significant characters but of varying degrees of constancy. Ecological conditions sometimes influence greatly the general appearance of a species and probably account for variability in many of these characters.

Some groups and species can be more readily distinguished by the mature leaves and fruit than in the flowering state, but the converse is also sometimes true. Perhaps mature fruit affords the best material for recognizing the groups, and often species may be

distinguished by this alone, but in all of the larger groups there are species in which the fruit is scarcely typical, or in which it is variable in size, shape or color, or sometimes in the thickness and consistency of the flesh, size of the calyx or number of the nutlets. The nest of nutlets often furnishes a definite clue to the group, but it is far too variable in some cases and there is too close a similarity in others to make it of much value in distinguishing species.

The leaves are parts of the plant that are nearly always available for study, and in a large proportion of cases, if specific lines are drawn fairly broadly, they possess recognizable differences. In fact, most of the sections or groups are distinguishable by the leaves alone. Of course it would be impossible to base a system of classification in so large a genus wholly, or even mainly, on leaf characters, but they perhaps furnish as many good characters, if both those of the fruiting branches and vigorous shoots, which often vary widely, are taken into account, as any other single feature, and they should be carefully considered in keys and descriptions.

It would have greatly simplified matters if any single organ or character, like the anther color, pubescence, glands, leaves or nutlets, were of constant value or varied consistently throughout the genus, but nature does not seem to work along lines of uniformity but upon those of the greatest diversity, and so it becomes impossible to follow any altogether uniform scheme in attempting to classify so large and variable a group as *Crataegus* into recognizable units. Any scheme adopted must be more or less eclectic and should recognize the fact that morphological characters that appear to be the most important in one section may not have equal value in another, and that each species is more or less a problem in itself.

From the foregoing I think it is apparent that the task of revising a genus of the size of *Crataegus* is a somewhat formidable one, and also one in which, with our present state of knowledge, no absolute finality can be expected. In some degree this is probably true of all taxonomic work. But it would seem that such a revision is urgently needed and that enough progress has now been made in understanding the genus to carry it out along conservative lines, that will neither seek to reduce arbitrarily species by throwing together as synonyms forms that are clearly recognizable, nor to maintain as species such as have proven to have been based on inconstant distinctions or morphological characters too slight or obscure to be worthy of specific rank. Such a treatment, while we cannot hope to devise a plan that will make a simple problem of a group of such large size and complexity and wide geographical

range, may at least do something towards simplifying it to a point where it will not be a hopeless task for the interested student to arrive at some knowledge of the principal forms or species, and if he is not particularly concerned with all the minor ones, he may do so without the expenditure of an unreasonable amount of time and study.

HERBARIUM, ARNOLD ARBORETUM
HARVARD UNIVERSITY